The understorey of gorgonian forests in mesophotic temperate reefs

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Abstract

1. In the Mediterranean Sea, dense populations of the gorgonian *Paramuricea clavata* shape marine animal forests characterizing the seascapes of coralligenous habitats. Despite the concerns for its health, due to several anthropogenic threats and recent mass mortality events mainly triggered by thermal anomalies, the understorey of its forests and the ecological processes they promote are still little known. Here, the abundance and composition of epibenthic assemblages inside and outside *P. clavata* forests were investigated across the central and western Mediterranean Sea, by applying a multifactorial sampling design.
2. In spite of the large variability in the structures of epibenthic assemblages at local and regional scales, the gorgonian understoreys share some common features, such as higher abundances of calcareous builder organisms and a reduced invasion by the non-indigenous alga *Caulerpa cylindracea*, compared to the adjacent unforested rocky bottoms. *P. clavata* showed non-linear density-dependent relationships with algal turfs and non-encrusting algae belonging to the genus *Peyssonnelia*. Moreover, by entrapping benthic mucilaginous aggregates with their branches, these gorgonians risk topical necrotic lesions but may reduce the suffocation risks for understorey organisms.
3. Overall, *P. clavata* forests may enhance bioconstruction processes and increase resistance and resilience of the benthic assemblages in the Mediterranean coralligenous habitats. This species and its forests, together with their understoreys, should be considered as essential elements of the Mediterranean Sea ecology, and therefore worthy of specific and effective protection measures.
4. Conservation strategies should reduce the risk of mechanical damage by regulating fishing activities, anchorages and scuba diving where gorgonian forests are present. Moreover,

when evident alterations are documented restoration actions should be implemented to recover gorgonian forests integrity.

Keywords: alien species, benthos, biodiversity, climate change, endangered species, invertebrates, subtidal

1 Introduction

In many marine habitats erect organisms may form dense populations resembling small terrestrial forests. They include canopy-forming algae (e.g. kelps, fucoids), but also branched sessile invertebrates (e.g. sponges, cnidarians, bryozoans) able to form dense mono- or pluri-specific "animal forests" (*sensu* Rossi, Bramanti, Gori, & Orejas Saco del Valle, 2017). Forests forming species directly or indirectly affect availability of abiotic and biotic resources by structural changes and therefore may be considered ecosystem engineers (Jones, Lawton, & Shachak, 1994; reviewed in Romero, Gonçalves-Souza, Vieira, & Koricheva, 2015). Terrestrial forest trees control the understorey by providing favourable microclimates, with less fluctuations of environmental variables (e.g. humidity, temperature, organic matter, nutrient, shading) compared to habitats outside tree assemblages, and by driving interactions among animals and plants (Wright, 2002). In the marine environment, kelp forests and the multitude of species interactions that they support may control ecosystem structure and functioning, mitigating environmental stress and enhancing resistance towards habitat loss or fragmentation (e.g. Bennett et al., 2015; Steneck et al., 2002). In kelp forests, sedimentation and accumulation of detritus (Airoldi, 2003; Duggins & Eckman, 1994) are considered key features in structuring benthic assemblages. Moreover, shading effects (Arkema, Reed, & Schroeter, 2009; Clark, Edwards, & Foster, 2004) and depth gradient (Graham, 2004; Rodgers & Shears, 2016) control their food webs, driven by the primary production provided by kelps and their epiphytes.

Ecological processes in terrestrial and kelp forests have been extensively investigated, while little is known about marine animal forests. Marine animal forests are made by dense assemblages of benthic suspension-feeders, filtering large quantities of seston and substantially contributing to the benthic-pelagic coupling (Gili, Coma, Orejas, López-González, & Zabala, 2001; Gili & Coma, 1998). They include sponge gardens (Marliave,

74 Conway, Gibbs, Lamb, & Gibbs, 2009), mono-specific forests of hydroids (Di Camillo et al.,
75 2013; Rossi, Bramanti, Broglio, & Gili, 2012), black corals (e.g. Bo, Canese, & Bavestrello,
76 2014; Ingrassia et al., 2016), mesophotic zoantharians (e.g. gold coral) and gorgonians
77 (Cartes, LoIacono, Mamouridis, Lopez-Perez, & Rodriguez, 2013; Cerrano et al., 2010). One
78 of the most peculiar elements characterizing Mediterranean coralligenous habitats
79 (mesophotic biogenic reefs, sensu Ballesteros, 2006) are the forests of the gorgonian
80 *Paramuricea clavata* (Risso 1826) (Musard et al., 2014). *P. clavata* is a long-lived, slow-
81 growing species (Linares, Doak, Coma, Díaz, & Zabala, 2007). Colonies, irregularly branched
82 and purple/yellow in colour, may be more than 1.5 m in height and over 100 years old
83 (Linares, Doak, Coma, Díaz, & Zabala, 2007). Pristine forests may reach densities of greater
84 than 50 colonies m^{-2} and dry masses greater than 1,700 g m^{-2} (Coma, Ribes, Zabala, & Gili,
85 1998; Linares, Coma, Garrabou, Díaz, & Zabala, 2008). Biology and ecology of this species
86 have been well studied: geographic and bathymetric distributions (Boavida, Assis, Silva, &
87 Serrão, 2016; Di Camillo, Ponti, Bavestrello, Krzelj, & Cerrano, 2017; Gori et al., 2011;
88 Kipson et al., 2015; see also Supplementary Material S1, Figure S1.1 and Figure S1.2),
89 reproduction, growth, secondary production and survivorship (Coma, Ribes, Zabala, & Gili,
90 1998; Cupido et al., 2012; Cupido, Cocito, Sgorbini, Bordone, & Santangelo, 2008; Fava,
91 Bavestrello, Valisano, & Cerrano, 2010; Linares, Coma, & Zabala, 2008; Linares, Doak,
92 Coma, Díaz, & Zabala, 2007; Mistri & Ceccherelli, 1994; Santangelo et al., 2015), feeding
93 ecology (Cocito et al., 2013; Coma, Gili, Zabala, & Riera, 1994; Ribes, Coma, & Gili, 1999),
94 respiration rate (Coma, Ribes, Gili, & Zabala, 2002; Previati, Scinto, Cerrano, & Osinga,
95 2010), and population genetic structure (Mokhtar-Jamai et al., 2011; Perez-Portela et al.,
96 2016; Pilczynska, Cocito, Boavida, Serrao, & Queiroga, 2016).
97 Integrity of *P. clavata* forests, however, is threatened by fishing lines and nets,
98 anchorages and recreational divers causing mechanical damage (Bavestrello, Cerrano, Zanzi,

& Cattaneo-Vietti, 1997; Linares & Doak, 2010; Markantonatou, Marconi, & Cerrano, 2016; Tsounis et al., 2012), suffocation by mucilaginous benthic aggregates (Giuliani, Virno Lamberti, Sonni, & Pellegrini, 2005; Mistri & Ceccherelli, 1996a), invasion from non-indigenous species (Cebrian, Linares, Marschal, & Garrabou, 2012), and increase in water turbidity and sedimentation rates due to run-off as a result of bad land management (Mateos-Molina et al., 2015). Moreover, gorgonian forests are threatened by global climate change-related disturbances such as increased frequency of exceptional storms (Teixido, Casas, Cebrian, Linares, & Garrabou, 2013) and thermal anomalies (Cerrano & Bavestrello, 2008; Linares, Coma, Garrabou, Díaz, & Zabala, 2008) that may induce physiological stress and increase their susceptibility to pathogens (Calvo et al., 2011; Rivetti, Fraschetti, Lionello, Zambianchi, & Boero, 2014; Vezzulli, Pezzati, Huete-Stauffer, Pruzzo, & Cerrano, 2013). The latter, coupled with reduced food availability due to the stratification of the water column in summer, seem to lie at the basis of the gorgonian mass mortality events recorded in recent decades in the north-western Mediterranean Sea (Calvo et al., 2011; Cerrano et al., 2000; Crisci, Bensoussan, Romano, & Garrabou, 2011; Garrabou et al., 2009; Huete-Stauffer et al., 2011; Linares et al., 2005; Martin, Bonnefort, & Chancerelle, 2002).

Currently, many *P. clavata* forests are fragmented in patches and considered in strong regression as a result of mass mortality events that repeatedly affected this long-lived, slow growing and low resilient species (Cerrano et al., 2005; Cupido et al., 2009; Linares et al., 2005). Concerns for gorgonian forests, and for the consequences of their loss on the associated assemblages and on the ecological processes occurring in the understorey are rising, even if little is known on the structure, diversity and abundances of the benthic assemblages associated to *P. clavata* forest. Manipulative experiments have highlighted that *P. clavata* forests significantly affect the early-stage recruitment of sessile epibenthic

assemblages, although effects may vary across sites exposed to different environmental conditions (Ponti et al., 2014).

The aims of the present study were to explore spatial patterns of epibenthic assemblages inhabiting the understorey of Mediterranean *P. clavata* forests, compared to adjacent not forested rocky areas, and to shed light on the conservation needs of this habitat-forming species to preserve biodiversity of coralligenous habitats.

2 Materials and methods

2.1 Sampling design and survey method

Epibenthic sessile assemblages inside and outside *Paramuricea clavata* forests were investigated by applying a multifactorial sampling design. Nine sites were randomly selected among those with a high abundance of *P. clavata*, as reported in the Reef Check database (Cerrano, Milanese, & Ponti, 2017; see Supplementary Material S1, Figure S1.1) (Figure 1). At each site four areas inside and four outside *P. clavata* forests, having similar orientation, inclination and depth (± 3 m), were randomly selected. Four photographic samples (21 × 28 cm) were collected within each area (Figure 2a) using either a Canon PowerShot G12 or a Canon PowerShot G15 digital cameras (10 to 12 Mpixel, respectively) equipped with an aluminium underwater case, S-TTL strobe (Inon D-2000) and a custom stainless steel frame. Inside gorgonian forests height and percentage cover of *P. clavata* colonies were measured in the field and by photographic samples (50 × 50 cm), respectively (Figure 2b).

Percentage cover of sessile organisms was quantified by superimposing a grid of 400 equal-sized squares, using the software PhotoQuad (Trygonis & Sini, 2012). Although several software are available to estimate the abundance of organisms in photographic samples, such as SeaScape, based on picture segmentation (Teixido et al., 2011), and CPCe, based on random points count (Kohler & Gill, 2006), PhotoQuad was chosen because it allows to

148 define the accuracy of the percentage cover estimation, based on the number of cells in the
149 superimposed grid, and does not set limits to the maximum number of identifiable species, as
150 occurs counting a set of random points. Percentage cover was related to the total readable area
151 of each image, obtained by subtracting dark and blurred zones or portions covered by motile
152 organisms as in Ponti, Fava, & Abbiati (2011). Organisms were identified to the lowest
153 possible taxonomic level, by comparisons to close-up photos and voucher specimens collected
154 in previous studies (e.g. Ponti, Fava, & Abbiati, 2011; Ponti et al., 2014), and grouped into
155 morpho-functional groups (modified from Casas-Güell, Teixidó, Garrabou, & Cebrian, 2015;
156 Garrabou, Ballesteros, & Zabala, 2002; Teixido, Garrabou, & Harmelin, 2011). All calcifying
157 taxa were also included in the builder group.
158
159 **2.2 Data analysis**
160 Differences in height and percentage cover of *Paramuricea clavata* forests between sites were
161 assessed by one-way Analysis of Variance (ANOVA, $\alpha = 0.05$; Underwood, 1997).
162 Benthic assemblage similarities were calculated for each pair of samples using the
163 Bray-Curtis coefficient applied to square root-transformed percentage cover data and
164 excluding *P. clavata* from the analysis (Clarke, 1993). Similarity patterns of benthic
165 assemblage inside and outside gorgonian forest and among sites were represented by both
166 unconstrained ordination plot, using the Principal Coordinate Analysis (PCoA; Gower, 1966),
167 and constrained ordination plot, using the Canonical Analysis of Principal coordinates (CAP;
168 Anderson & Willis, 2003), calculated on the centroids of similarities among replicates from
169 the same sampling area. CAP detects the axis that best discriminate between the two *a priori*
170 groups, i.e. benthic assemblages inside and outside gorgonian forest.
171 The possible relationship between the similarity patterns of the benthic assemblages
172 and environmental conditions and geographical locations (see Supplementary Material S2,

Figure S2.1, Table S2.2) were investigated by multivariate multiple regression using the DistLM procedure that provides a step-wise conditional selection of predictor variables significantly correlated with the obtained similarity patterns (McArdle & Anderson, 2001). These relationships were graphically represented by vectors superimposed on the PCoA plot.

Differences in assemblage structures inside and outside gorgonian forest (Go: 2 levels, fixed), among sites (Si: 9 levels, random), in the interaction (Go × Si), and among areas nested in this interaction (Area(Go × Si)) were assessed by permutational multivariate analysis of variance (PERMANOVA, $\alpha = 0.05$; Anderson & ter Braak, 2003). When less than 999 unique values in the permutation distributions were available, asymptotical Monte Carlo *p*-values (p_{MC}) were used instead of permutational *p*-values. Results of the PERMANOVA test were reported along with the estimated component of variation, in percentage of the total, allowing to compare the relative importance of different terms in the model (Anderson, Gorley, & Clarke, 2008).

Species richness (as number of species, *S*), species diversity (as Hill's diversity number *N1* = Exp *H'*, where *H'* is the Shannon's index based on natural logarithm) and the corresponding evenness component (as *N10* = *N1*/*S*) were calculated for each sample (Magurran, 2004). *N1* represent the 'effective number of species' of an assemblage, i.e. the species richness of a perfectly even assemblage (all species equally common) with the same diversity as the original assemblage (Hill, 1973).

Differences in single species percentage cover, morpho-functional groups percentage cover and species diversity indices were assessed by mixed multifactorial ANOVA ($\alpha = 0.05$) following the same design adopted for PERMANOVA. Cochran's C test was used to check the assumption of homogeneity of variances and, when necessary, data transformations were applied. If variances were slightly heterogeneous even after transformations (Cochran's C test $0.05 > p > 0.01$), the analyses were run at $\alpha = 0.01$ for significance test, while when variances

were highly heterogeneous (Cochran's C test $p < 0.01$), the analyses were conservatively run at $\alpha = 0.001$ (Underwood, 1997). In the ANOVA, when the term Go × Si was not significant ($p > 0.25$) it was pooled with the term Area(Go × Si) (Underwood, 1997). When the term Go × Si was significant, the Student–Newman–Keuls (SNK) method was used for the *post-hoc* comparisons.

Possible relations between the percentage cover of *P. clavata* and those of other taxa were explored by local polynomial regression fitting (LOESS), which is a smoothing method that summarizes the association between variables by fitting a multitude of regression models to adjacent subsets of the data (Cleveland & Devlin, 1988). For this purpose, percentage cover data inside gorgonian forests were averaged by area (i.e. 4 areas per site).

Multivariate analyses were performed using PRIMER 6 with PERMANOVA+ add-on package (Anderson, Gorley, & Clarke, 2008). LOESS and univariate analyses were made in R (R Core Team, 2017) with GAD, a specific package for General ANOVA Designs (Sandrini-Neto & Camargo, 2012). Mean values were always reported along with their standard errors (s.e.).

3 Results

3.1 The investigated gorgonian forests

The study sites were located over a wide geographical area, which spans 5.6° in latitude and 8.2° in longitude, from the north-western Mediterranean Sea (P.te Causinière at Cap Ferrat, Villefranche-sur-Mer and Colombara at Portofino, in the Ligurian Sea, Punta delle Cannelle, Capo Calvo, Picchi di Pablo and Scoglio del Remaiolo at Elba Island in the central Tyrrhenian Sea) to the central Mediterranean (Punta San Paolo at Ustica Island) and to the northern Adriatic Sea (Zverinac Južni Rt and Rivanjski Kanal in Croatia). At study sites, gorgonian forests occur at different depths, with upper limits from 22 to 40 m, either on

223 vertical or horizontal substrates, with different orientations. Geological and environmental
224 features at each site were reported in the Supplementary Material (S2, Figure S2.1, Table S2.1
225 and S2.2).
226 Gorgonian forests significantly differed between study sites both in terms of colony
227 height ($F_{8,27}$ = 6.38, p = 0.0001) and percentage cover ($F_{8,27}$ = 2.48, p = 0.037). The mean
228 gorgonian height ranges from 25.4 ± 4.3 cm to 122.1 ± 22.6 cm; while their mean percentage
229 cover ranges from 22.3 ± 5.1 % to 56.8 ± 7.4 % (Figure 2c,d; Figure 3).
230
231 **3.2 Epibenthic assemblages inside and outside gorgonian forests**
232 Besides *Paramuricea clavata*, 97 taxa were recorded and quantified, of which 45 were
233 identified to species level. The allocation of taxa to morpho-functional groups has been
234 reported in the Supplementary Material (S3, Table S3.1).
235 The most abundant and widely distributed taxa were encrusting calcareous
236 rhodophytes belonging to Corallinaceae and Peyssonneliaceae families, and erect algae such
237 as *Flabellia petiolata* (Turra) Nizamuddin 1987, *Pseudochlorodesmis furcellata* (Zanardini)
238 Børgesen 1925 and *Halimeda tuna* (J.Ellis & Solander) J.V.Lamouroux 1816. Some species,
239 though locally abundant, were found only in nearby sites. It was the case of the colonial
240 ascidians *Polycitor adriaticus* (Drasche 1883) and *Aplidium conicum* (Olivi 1792) that were
241 recorded only in the northern Adriatic Sea (Figure 2c), and of the invasive alga *Caulerpa*
242 *cylindracea* Sonder 1845 that was found at Elba Island (Figure 2e).
243 Benthic assemblages showed a large variability among sampling areas (i.e. local
244 scale), which accounts for 19.7% of the total observed variation, and among sites (28.1% of
245 the total variation). Significant differences were also found in relation to the presence of
246 gorgonian forest across sites (19.0% of the total variation; Table 1). The variability of the
247 benthic assemblages associated with the presence/absence of the gorgonian per se,

248 independently from the geographical location, accounts for the 9.4% of the total observed
249 variation. Patterns of similarity among assemblages were strongly affected by differences
250 among sites rather than inside and outside gorgonian forests, as it is well represented in the
251 PCoA ordination plot (Figure 4a). In the unconstrained plot, the data cloud is driven by the
252 large geographical differences in assemblage structures, represented by the correlation vector
253 of the longitude, as well as by depth and substrate inclination. Inclination, depth and latitude
254 were selected by the DistLM step-wise procedure as the best combination of variables
255 significantly correlated to the obtained similarity pattern and together explain 46.8% of the
256 total variation in benthic assemblages. The variability among sites tends to mask the effects of
257 the presence of gorgonians, however detected by PERMANOVA test (Table 1). Conversely,
258 the constrained ordination plot, obtained by CAP, revealed a clear differentiation between
259 assemblages inside and outside gorgonian forest, with a large canonical correlation of 0.87
260 (Figure 4b).

261 Few species, individually analysed, showed a clear pattern in relation to the
262 occurrence of gorgonian forest. The green algae *Codium bursa* (Olivi) C.Agardh 1817 was
263 found at five sites out of nine, and always only outside *P. clavata* forest. The yellow
264 gorgonian *Eunicella cavolini* (Koch 1887) was found at six sites out of nine, and at five of
265 these was present only inside *P. clavata* forest. However, ANOVA tests failed to detect a
266 significant effect of the gorgonian forest on the abundance of *C. bursa* and *E. cavolini* due to
267 the paucity of data and heterogeneity of variances (Table 2). Overall, the percentage covers of
268 encrusting sponges (from zero to 9.9 ± 1.6%) and encrusting bryozoans (from zero to 6.1 ±
269 1.5%) were very variable at the local and regional scales, i.e. among areas and sites, and in
270 both cases they were significantly more abundant inside the gorgonian forests (Table 2,
271 Figure 5a,b). The percentage covers of erect bryozoans varied from 0.03 ± 0.03% to 6.1 ±
272 3.0% and showed a less clear pattern with a large variability at the local scale. Their

abundance inside and outside gorgonian forests was not consistent across sites (Table 2). The SNK test revealed that their percentage covers were significantly higher inside the gorgonian forests at three sites, while at the six other sites no differences were detected (Figure 5c). Mixed turf, which includes many filamentous algae and hydroids, showed percentage covers ranging from 6.6 ± 3.3% and 52.6 ± 4.7% with significant variability at local scale (Table 2). Its abundance inside and outside gorgonian forests was not consistent across sites. In this case, the SNK test revealed that its percentage covers were significantly higher outside the gorgonian forests at seven sites, while at the two remaining sites no differences were detected (Figure 5d). Percentage cover of the encrusting calcareous rhodophytes (ECR), ranging from 1.3 ± 0.6% to 26.7 ± 3.2%, significantly varied among sites and showed higher values inside gorgonian forest (Table 2, Figure 5e). Similar results were obtained by summing encrusting calcareous rhodophytes with all the other builder organisms that may contribute to the coralligenous framework (Table 2, Figure 5f).

Percentage covers of green algal turfs and non-encrusting algae belonging to the genus *Peyssonnelia*, although not significantly different between inside and outside the gorgonian forests, showed a peculiar pattern in relation to the cover of *P. clavata* inside the forests. At low gorgonian cover (up to 30%), green algal turfs seemed to be facilitated by *P. clavata*, while *Peyssonnelia* spp. were not affected (Figure 6a,b). At higher gorgonian cover, the percentage covers of both algal groups decreased dramatically, down to about 10%. The non-indigenous alga *Caulerpa cylindracea* was found only at three sites located at Elba Island. At these three sites, the percentage cover of *C. cylindracea* showed large variability at the local scale (i.e. significant differences among areas) and significantly lower values inside the gorgonian forests (Table 2, Figure 7a). Mucilaginous aggregates were found at only three sites: Colombara at Portofino, Punta San Paolo at Ustica Island and Picchi di Pablo at Elba Island (Figure 2f). At these three sites, the percentage cover of these aggregates showed large

298 variability at the local scale and a significant variation across sites and inside *vs* outside
299 gorgonian forest (Table 2). The SNK test revealed that percentage covers were significantly
300 higher outside the gorgonian forests at two sites out of three sites (Figure 7b).
301 All the species diversity indices (*S*, *N1* and *N10*) showed significant variability at local
302 scale, i.e. among areas within the interaction between site and gorgonian forest. Species
303 richness (*S*) and evenness (*N10*) significantly differed among sites. Overall, all indices were
304 significantly higher inside the gorgonian forests (Table 2, Figure 8).
305

306 **4 Discussion**

307 This study compared the epibenthic assemblages inside and outside gorgonian forests
308 across a broad range of central and western Mediterranean coralligenous habitats, differing in
309 environmental conditions and belonging to different biogeographic sectors (sensu Bianchi &
310 Morri, 2000). Gorgonian forests vary in colony density, and dwell on rocky substrates
311 differing in inclination, orientation and depth. Overall, understorey assemblages of these
312 animal forests showed a large variability at different spatial scales. The percentages of
313 component of variation of benthic assemblage structures at local (i.e. areas) and regional (i.e.
314 sites) scales were comparable to those obtained in a previous study carried out by means of
315 photographic samples inside *P. clavata* forests in the NW Mediterranean Sea (Casas-Güell,
316 Teixidó, Garrabou, & Cebrian, 2015). None of the species found in this study are exclusive of
317 either forested or not forested habitats, nor closely associated with the presence of *P. clavata*.
318 Nevertheless, at the local scale, the structures of the epibenthic assemblages significantly
319 differed between inside and outside the gorgonian forests.
320 The Mediterranean yellow gorgonian *Eunicella cavolini* is often associated with the *P.*
321 *clavata* forests. Interspersion between colonies of *E. cavolini* and *P. clavata*, as observed in
322 the present study, is a common finding through all the Mediterranean Sea (Di Camillo, Ponti,

323 Bavestrello, Krzelj, & Cerrano, 2017). This suggests a large overlap in their ecological niche
324 and limited interspecific competition, at least at low colony densities. *E. cavolini* colonies are
325 smaller in size, have a slower growth rate, an higher P/B ratio, and a lower turnover rate
326 compared to *P. clavata* (Coma, Ribes, Zabala, & Gili, 1998 and references therein). These
327 two gorgonians are affected by the same local and global threats (Cerrano et al., 2000;
328 Garrabou et al., 2009; Sini, Kipson, Linares, Koutsoubas, & Garrabou, 2015), although *E.*
329 *cavolini*, in a field experiment, showed greater resistance to thermal stress, with a lower
330 mortality and a higher recovery capacity compared to *P. clavata* (Fava, Bavestrello, Valisano,
331 & Cerrano, 2010). Forests of *P. clavata* being larger in size may protect *E. cavolini* and other
332 fragile species, such as erect bryozoans, from mechanical damage (e.g. fishing lines, nets and
333 divers), as already documented for *Pentapora fascialis* (Pallas 1766) by Garrabou, Sala,
334 Arcas, & Zabala (1998).

335 Compared to the unforested rocky bottoms, the understorey of *P. clavata* forests host
336 higher percentage covers of encrusting sponges, encrusting bryozoans and encrusting
337 calcareous rhodophytes. All of them are relevant components of the Mediterranean
338 coralligenous habitats and contribute to their frameworks (Ballesteros, 2006). Recruitment of
339 encrusting sponges and encrusting bryozoans may be facilitated by the presence of *P. clavata*,
340 as consistently observed in early-stage recruitment experiments carried out in the Ligurian
341 and the Tyrrhenian Sea (Ponti et al., 2014). The reduction of light intensity and sediment
342 accumulation induced by gorgonian branches may favour the competitive success of
343 encrusting calcareous rhodophytes, as observed under canopies of marine plant and
344 demonstrated by manipulating this physical factors in subtidal rocky habitats (Airoldi, 2003;
345 Connell, 2005; Connell, 2003; Irving & Connell, 2002).

346 Overall, by summing all organisms able to deposit calcium carbonate it turns out that
347 these forests support higher abundances of builder organisms. These findings suggest that

348 gorgonian forests may largely contribute to maintaining and developing coralligenous
349 biogenic habitats. On the contrary, mixed turfs of filamentous algae and hydroids, which
350 normally tend to compete for space with encrusting sponges, encrusting bryozoans and
351 encrusting calcareous rhodophytes, were often more abundant outside the gorgonian forests.
352 *Codium bursa*, was found only outside the forests. The growth of this long-lived and
353 slow-growing alga, is generally limited by nutrient availability (especially phosphorus), rather
354 than by light (Vidondo & Duarte, 1995). This suggests that the limiting effect of *P. clavata*
355 towards this seaweed go well beyond the simple shading and likely acts at the early
356 recruitment stage.
357 At high gorgonian density, edaphic conditions (e.g. physical factors such as light,
358 currents, sedimentation rates) may be strongly modified, increasing habitat complexity that
359 supporting many necto-benthic organisms (Cerrano et al., 2010; Ponti et al., 2016; Valisano,
360 Notari, Mori, & Cerrano, 2016). This study highlighted that the direct or indirect effects of the
361 gorgonians on the abundance of other species, as green algal turfs and non-encrusting
362 peyssonneliacean algae, may vary by gorgonians density, in terms of percentage cover.
363 Indeed, the effects of gorgonians on erect and filamentous algae could vary with colony
364 densities, sites and depths, as observed in the early-stage recruitment experiments (Ponti et
365 al., 2014). The reduction in the abundance of some algal species seems to occur when the
366 gorgonian cover exceeds 30%. This value could be considered a threshold to detect a shading
367 effect and therefore a reference value in the assessment of the health status of the forests.
368 However, density-dependent interactions in marine animal forests are far from being
369 understood and deserve further investigations.
370 Higher values of species diversity indices were found inside gorgonian forests,
371 compared to surrounding rocky bottoms. This trend is consistent across the investigated

geographical area, corroborating the hypothesis of a positive relationship between three-dimensional habitat complexity and species diversity (Kovalenko, Thomaz, & Warfe, 2012).

4.1 A focus on the non-indigenous species *Caulerpa cylindracea*

Non-indigenous species (NIS) have been recognized as a threat to the integrity of Mediterranean native communities. Establishment of NIS can drastically change the structure of marine communities, affecting species growth rates, survival and reproduction (Butchart et al., 2010; Occhipinti-Ambrogi, 2007). The green alga *Caulerpa cylindracea* is listed among the most threatening Mediterranean invaders (Streftaris & Zenetos, 2006), and represents one of the major concerns for the coralligenous habitats (Piazzi, Balata, & Cinelli, 2007; Piazzi, Gennaro, & Balata, 2012). Manipulative experiments showed that the presence of *C. cylindracea* negatively affects the *Paramuricea clavata* fitness by increasing the percentage of necrosis and lowering biomass and survivorship (Cebrian, Linares, Marschal, & Garrabou, 2012). However, the role of gorgonian forests in preventing the settlement and invasion of *C. cylindracea* has never been investigated. At all sites where it occurred *C. cylindracea* was significantly less abundant inside gorgonian forests. The result seems fairly robust and suggests a resistance of the gorgonians to the invasion of this seaweed. Piazzi, Balata, Bulleri, Gennaro, & Ceccherelli (2016), in a recent review on biotic and abiotic interactions of *C. cylindracea* in the Mediterranean Sea, suggested that canopy-forming algae and seagrasses may limit the spread of *C. cylindracea* by reducing photosynthetic performance by shading. Gorgonian forests may cause similar shadow effects. Moreover, *P. clavata* may directly or indirectly reduce the recruitment of *C. cylindracea* by releasing allelochemicals (Rodriguez, 1995) or limiting the abundance of algal turfs, which may enhance the spread of the invader (Piazzi, Balata, Bulleri, Gennaro, & Ceccherelli, 2016 and references therein).

4.2 Entrapment of mucilaginous aggregates

Developments of mucilaginous aggregates are recurrent events in the Mediterranean Sea (Rinaldi, Vollenweider, Montanari, Ferrari, & Ghetti, 1995; Sartoni et al., 2008). Deposition of mucilaginous aggregates on the seabed may cause severe damage to many benthic organisms, by reducing light availability, suffocating sessile invertebrates and establishing anoxic conditions (Schiaparelli, Castellano, Povero, Sartoni, & Cattaneo-Vietti, 2007). Gorgonians are very sensitive to mucilage, which can cause necrosis of coenenchyme and leave portions of axial skeleton bare (Giuliani, Virno Lamberti, Sonni, & Pellegrini, 2005; Mistri & Ceccherelli, 1996a). *Paramuricea clavata* colonies may recover from damage caused by mucilage in a few years through recruiting juvenile colonies (Mistri & Ceccherelli, 1996b). The present study shows that gorgonians may reduce the accumulation in the understorey by trapping the mucilaginous aggregates with their branches. Gorgonian forests, although at expense to themselves, may therefore limit the damage from suffocation to many associated benthic invertebrates.

5 Conclusions

The ecological role played by habitat-forming species cannot be easily disentangled, either from a physical or biological perspective. Generally, increased habitat complexity leads to higher species diversity in the associated assemblages, by increasing the available space and the number of microhabitats (Kovalenko, Thomaz, & Warfe, 2012). Moreover, the habitat complexity built up by ecosystem engineers induces physical changes, but may also modify many biological processes, with unpredictable ecological effects (Kelaher, 2003). Although the mechanisms underlying these processes are still not well known, forests of *Paramuricea clavata*, besides modifying microscale hydrodynamics, may provide additional food resources, being an effective suspension feeder able to modify littoral marine food webs

(Coma, Gili, Zabala, & Riera, 1994; Gili & Coma, 1998), increase refuges and available surface area (Ponti et al., 2016; Valisano, Notari, Mori, & Cerrano, 2016), as well as affect recruitment processes (Ponti et al., 2014). According to the present results, these animal forests are supporting high species diversity and promote bioconstruction processes in their understorey. Presence of long-lived gorgonians may contribute to reducing the temporal variability of epibenthic assemblages, as already reported for Mediterranean coralligenous habitats (Casas-Güell, Teixidó, Garrabou, & Cebrian, 2015; Teixido, Garrabou, & Harmelin, 2011). Indeed, healthy gorgonian forests may also oppose to the spread of non-indigenous species and mitigate the effects of adverse events, like mucilage formations. Gorgonian species play an ecological role that goes well beyond the aesthetic value, which attracts a large number of recreational divers (Musard et al., 2014). The obtained results support the concern raised by several scientists about the loss of habitat complexity caused by extensive mass mortalities of Mediterranean gorgonians (Cerrano & Bavestrello, 2008). The fragmentation and the local disappearance of gorgonian forests could cause severe and sudden modifications of associated epibenthic communities. It may lower species diversity, alter ecosystem functioning, and reduce the resistance and resilience of the assemblages with concomitant losses of ecological goods and services, over different spatial and temporal scales. *Paramuricea clavata* is considered a "vulnerable" species according to the Mediterranean Red List (ver. 3.1) provided by IUCN, mainly because of its low recruitment rate, and the *facies* with *P. clavata* is listed in the habitats that deserve special protection under the Barcelona Convention (RAC/SPA, Tunis). Evidence from this and many other studies strongly suggest the need to consider the health status of this species and of the forests it shapes, threatened by several anthropogenic disturbance and by the global climate changes, as essential elements of the ecological dynamics of the Mediterranean Sea, and therefore worthy of specific and effective transboundary protection measures. The European Marine

447 Strategy Framework Directive (2008/56/EC), the environmental pillar of the Blue Growth
448 strategy, defines the need of each member state to reach Good Environmental Status (GES) of
449 their marine waters. This achievement should require an urgent regulation of fishing activity,
450 anchorages and scuba diving where gorgonian forests are present and restoration activities
451 when evident alterations are documented. The results here presented clearly indicate that *P.*
452 *clavata* represent a key species to maintain the GES of the Mediterranean temperate reefs, the
453 coralligenous habitats.
454 Our results suggest that the health status of *P. clavata* forests could be monitored by using
455 physical and structural descriptors, related to the magnitude of their positive effects on the
456 complexity of benthic assemblages. The descriptors should include depth (range or upper
457 limit of the forest), bottom inclination and orientation, mean colony height and percentage
458 cover of the colonies. Furthermore, the percentage cover of bioconstructors in the understorey
459 could be considered as a proxy of the effectiveness protection offered by gorgonians to the
460 benthic community. Bioconstructors are a key component in maintaining coralligenous
461 habitats and their species diversity. Other important aspects that should be monitored are the
462 degree of fragmentation of the forest, the extent of bare skeletons and necrotic portions of
463 coenenchyme. Human impacts on gorgonian forest could be quantified by measuring the
464 amount of fishing lines and nets entangled in colonies, which may cause lesions, while the
465 quantity of epibionts may provide information on how long they have been damaged by
466 humans or by natural events.
467 Several actions should be undertaken to protect gorgonian forests starting from the reduction
468 of local human disturbances (both al the coast and inland; Mateos-Molina et al., 2015),
469 establishing and enforcing properly designed and regulated marine protected areas
470 (Arizmendi-Mejía et al., 2015; Coma, Pola, Ribes, & Zabala, 2004; Linares & Doak, 2010),
471 and considering the aesthetic values of seascapes in conservation policies (Chimienti et al.,

2017). However, while much can be done for the conservation of healthy marine animal forests, methodologies for the maintenance and restoration, that have been successfully applied in coral reefs (e.g. Epstein, Bak, & Rinkevich, 2001; Jaap, 2000; Rinkevich, 2005; Young, Schopmeyer, & Lirman, 2012), are not yet available for temperate gorgonian forests. Maintenance actions may consist in removing fishing lines and nets that have a prolonged action over time (Bavestrello, Cerrano, Zanzi, & Cattaneo-Vietti, 1997) and pruning the top of branches in order to remove lesioned and compromised parts, allowing for regrowth (Previati et al., 2011; Sánchez-Tocino, De La Linde Rubio, Lizana Rosas, Pérez Guerra, & Tierno De Figueroa, 2018). Transplantation techniques are under development (Fava, Bavestrello, Valisano, & Cerrano, 2010; Linares, Coma, & Zabala, 2008; Montero-Serra et al., 2018) and could be effective in order to restore lost and damaged forests. Owing to the continuous risks of thermal anomalies due to climate change, these restoring approaches should be addressed below the average depth of the summer thermocline. These approaches are very promising, especially if chronic and persistent human disturbances are removed before interventions. Integration of biological experiments with the eco-engineering approaches has been proved to be successful in restoration of coastal ecosystems and the possibilities to use it also on temperate mesophotic biogenic reefs should be properly explored.

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847

TABLE 1 PERMANOVA test on differences of epibenthic assemblage structures between inside and outside gorgonian forest (Go: 2 levels, fixed), among sites (Si: 9 levels, random), their interaction (Go × Si) and among areas within this interaction (Area(Go × Si)) (square root-transformed percentage cover data, Bray-Curtis coefficient). Estimated component of variation, in percentage of the total (CV%), was reported for each term of the model.

Source	df	SS	MS	Pseudo-*F*	*p*	Unique perms	CV%
Gorgonian forest (Go)	1	22,252	22,252.00	2.61	0.0280	9944	9.4
Site (Si)	8	235,020	29,378.00	12.89	0.0001	9856	28.1
Go × Si	8	68,109	8,513.60	3.74	0.0001	9823	19.0
Area (Si × Go)	54	123,080	2,279.20	3.76	0.0001	9539	19.7
Residual	216	130,930	606.16				23.7
Total	287	579,390					

TABLE 2 Summary of ANOVA tests. Data transformation: sqrt = square root; frt = four root. Degrees of freedom of numerator and denominator are given in parentheses. Significant levels were indicated by the following symbols: ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

	Cochran's C test	Gorgonian forest (Go)				Site (Si)				Go × Si				Area (Go × Si)				Res
	Transf.	MS	*F*	*p*		MS	*F*	*p*		MS	*F*	*p*		MS	*F*	*p*		MS
Codium bursa	none	18.39	4.69	0.062		3.92	0.88	0.540		3.92	0.88	0.540		4.45	0.97	0.542		4.60
	p <0.01		(1,8)				(8,54)				(8,54)				(54,216)			
Eunicella cavolini	none	92.35	6.66	0.033	*	16.98	2.01	0.063		13.87	1.64	0.135		8.46	1.41	0.047	*	6.02
	p <0.01		(1,8)				(8,54)				(8,54)				(54,216)			
Encrusting sponges	frt	7.56	8.04	0.022	*	4.18	8.33	0.000	***	0.94	1.88	0.083		0.50	2.25	0.000	***	0.22
	p ns		(1,8)				(8,54)				(8,54)				(54,216)			
Encrusting bryozoans	frt	9.48	12.48	0.008	**	4.11	10.25	0.000	***	0.76	1.89	0.080		0.40	2.14	0.000	***	0.19
	p ns		(1,8)				(8,54)				(8,54)				(54,216)			
Erected bryozoans	frt	16.72	16.58	0.004	**	2.20	4.66	0.000	***	1.01	2.14	0.048	*	0.47	2.21	0.000	***	0.21
	p ns		(1,8)				(8,54)				(8,54)				(54,216)			
Mixed turf	none	26'978.40	21.70	0.002	**	1'987.70	5.92	0.000	***	1'243.00	3.70	0.002	**	336.00	3.70	0.000	***	90.90
	p ns		(1,8)				(8,54)				(8,54)				(54,216)			
ECR	none	3'228.50	684.92	0.000	***	1'779.10	377.43	0.000	***	Pooled with				4.71	0.10	1.000		47.30
	p <0.01		(1,62)				(8,62)			Area (Go × Si)					(62,216)			
Builder organisms	sqrt	134.31	28.49	0.000	***	33.15	7.03	0.000	***	Pooled with				4.71	4.50	0.000	***	1.05
	p <0.01		(1,62)				(8,62)			Area (Go × Si)					(62,216)			
Caulerpa cylindracea	none	1'193.70	6.71	0.017	*	282.70	1.59	0.229		Pooled with				177.85	4.62	0.000	***	38.50
	p ns		(1,20)				(2,20)			Area (Go × Si)					(20,72)			
Mucilaginous algae	sqrt	169.09	5.08	0.153		26.59	4.09	0.034	*	33.290	5.13	0.017	*	6.49	5.27	0.000	***	1.23
	p ns		(1,2)				(2,2)				(2,18)				(18,72)			
S	none	308.35	14.90	0.005	**	61.88	5.68	0.000	***	20.70	1.90	0.079		10.89	1.96	0.000	***	5.55
	p ns		(1,8)				(8,54)				(8,54)				(54,216)			
N1	frt	0.77	20.74	0	**	0.04	2.56	0.02	*	0.04	2.4	0.03	*	0.02	1.69	0.01	**	0.01
	p <0.05		(1,8)				(8,54)				(8,54)				(54,216)			
N10	none	0.14	6.79	0.031	*	0.10	6.77	0.000	***	0.02	1.45	0.197		0.01	1.66	0.006	**	0.01
	p ns		(1,8)				(8,54)				(8,54)				(54,216)			

858 **Figures legends**

859

860 **FIGURE 1** Study area and study sites (circles): 1, P.te Causinière; 2, Colombara; 3, Punta
861 delle Cannelle; 4, Capo Calvo; 5, Picchi di Pablo; 6, Scoglio del Remaiolo; 7, Punta San
862 Paolo; 8, Zverinac Južni Rt; 9, Rivanjski Kanal (Mercator Projection, Datum WGS 84).

863

864 **FIGURE 2** Photographic sampling method (a, courtesy of Adelmo Sorci); a sampled area
865 inside a gorgonian forest at Punta San Paolo, Ustica Island (b); benthic assemblages at
866 Rivanjski Kanal, northern Adriatic (c); a dense gorgonian forest in the Tyrrhenian Sea (d);
867 some thalli of *Caulerpa cylindracea* at the basis of *Paramuricea clavata* at Punta delle
868 Cannelle, Elba Island (e); mucilaginous aggregates entrapped by gorgonian branches (f).

869

870 **FIGURE 3** Mean (± s.e.) height (a) and percentage cover (b) of *Paramuricea clavata* inside
871 the gorgonian forest at each study site.

872

873 **FIGURE 4** Unconstrained (a; PCoA) and constrained (b; CAP) ordination plots of benthic
874 assemblage data from inside and outside forests of the gorgonian *Paramuricea clavata* at 9
875 sites in the Mediterranean Sea. Each symbol represents the centroid of 4 areas with 4
876 replicated samples each. Vectors superimposed to plot (a) represent the correlations of
877 substrate inclination, site depth and longitude with the PCoA axes.

878

879 **FIGURE 5** Mean (± s.e.) percentage covers of encrusting sponges (a), encrusting bryozoans
880 (b), erect bryozoans (c), mixed turf (d), encrusting calcareous rhodophytes (ECR, e) and all
881 builder organisms together (f), inside and outside forests of the gorgonian *Paramuricea*
882 *clavata* at 9 sites in the Mediterranean Sea. Significant levels in SNK tests inside *vs*. outside

883 gorgonian forests within sites were indicated by the following symbols: * = $p < 0.05$; ** = $p <$
884 0.01; *** = $p < 0.001$.
885
886 **FIGURE 6** Polynomial regression fitting (LOESS) between percentage cover of *Paramuricea*
887 *clavata* and percentage cover of green algal turf (a) and non-encrusting algae of the genus
888 *Peyssonnelia* (b). The dashed lines delimit the confidence intervals at 95%.
889
890 **FIGURE 7** Mean (± s.e.) percentage covers of *Caulerpa cylindracea* (a) and mucilaginous
891 aggregates (b), inside and outside forests of the gorgonian *Paramuricea clavata* at 3 sites in
892 the Mediterranean Sea. Significant levels in SNK tests inside *vs*. outside gorgonian forests
893 within sites were indicated by the following symbols: * = $p < 0.05$; ** = $p < 0.01$; *** = $p <$
894 0.001.
895
896 **FIGURE 8** Mean (± s.e.) species richness (*S*, a), species diversity in terms of effective
897 number of species (*N1*, b) and the corresponding evenness component (*N10*, c), inside and
898 outside forests of the gorgonian *Paramuricea clavata* at 9 sites in the Mediterranean Sea.
899